merous eggs (3000 to 4000 per capsule) and the protoconch consists of 3¼ to 5¼ whorls (HUGHES & EMERSON, 1987: 357; TAYLOR 1975:394, pl. 67; REHDER, 1973:237, pl. 208). *Harpa* is known from the Neogene of France, Italy, the Caribbean, Peru, Fiji, and Japan. Like *Morum,* most of the living species of *Harpa, i.e.,* 8 of the 10 recognized species, are largely concentrated in the Indo-Pacific biogeographical region, with one species each in tropical eastern Pacific and eastern Atlantic waters (REHDER, 1973). Unlike *Morum,* however, 50% of the Indo-Pacific species extend eastward onto the Pacific Plate. Three of the four Pacific Plate *Harpa* (*H. harpa* Linnaeus, 1758; *H. amouretta* Roeding, 1798; and *H. major* Roeding, 1798) have extensive geographical ranges, occurring from east Africa to the Hawaiian Islands, with the last two taxa also known from the Marquesas Islands (REHDER, 1973; KAY, 1979; SALVAT & RIVES, 1980). The fourth of these species (*H. gracilis* Broderip & Sowerby, 1829) may be restricted to the Pacific Plate (Ellice Islands [Vuvalu] to the Tuamotus Archipelago and Marquesas Islands [AMNH 240922], and on Clipperton Island, REHDER, 1973:243), although a specimen of this species was recently attributed to Guam, in the Mariana Islands (*teste* Albert Deynzer, 1988). It is notable that the three species of *Harpa* (*H. harpa, H. amouretta,* and *H. major*) previously reported from Guam (*teste* B. D. Smith, 1986) are also found in the Hawaiian Islands (KAY, 1979:284). The Hawaiian fauna, however, lacks *Morum* as well as representatives of the Volutidae, Cancellariidae, Turbinellidae, and other groups of prosobranch gastropods that are mostly limited to a direct developmental mode (*cf.* SCHELTEMA, 1986:253).

The sharply contrasting distributional patterns of *Morum* and *Harpa* seemingly reflect the limited biological dispersal potential of most of the species of *Morum.* With the demise of the circumtropical Tethyan seaways, *Morum* was largely restricted in the Pacific tropics to the continental margins and the larger islands off the continental borderlands. This pattern of distribution has existed despite the fact that the major current circulation in the tropical Pacific has favored east to west dispersal pathways commencing in the late Neogene or perhaps much earlier (*cf.* NEWTON, 1988), whereas the Tethyan circulation was predominately west to east (*cf.* GRIGG, 1988).

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Seasonal, Diurnal, and Nocturnal Activity Patterns of Three Species of Caribbean Intertidal Keyhole Limpets (Mollusca: Gastropoda: *Fissurella*)

by

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Abstract. The activity patterns of three intertidal keyhole limpets, *Fissurella nimbosa* (Linnaeus, 1758), *F. nodosa* (Born, 1778), and *F. barbadensis* (Gmelin, 1791), were periodically observed on Isla de Margarita, Venezuela, from November 1986 to August 1987. Two-way factorial ANOVAs indicate significant interaction among seasons and species in distances the animals moved and in the number of movements they made during their feeding excursions. *Fissurella* spp. have grazing areas of approximately the same magnitude on a seasonal basis. These congeneric fissurellids exhibited homing behavior to a scar, which was generally located near the center of the feeding range. Homing was seen most frequently in populations of *F. barbadensis* and *F. nimbosa*, and to a lesser degree in *F. nodosa*. *Fissurella nodosa* grazed diurnally 75.8% of the time; nocturnal activity patterns accounted for 61% of the grazing in *F. nimbosa* and 98.2% in *F. barbadensis*. *Fissurella nimbosa* and *F. nodosa* most commonly grazed while awash during the rising or falling tides. *Fissurella barbadensis* also fed during this time, but more typically it grazed during high tides while submerged. The temporal and spatial patterns of *Fissurella* are discussed with reference to other intertidal grazers.

INTRODUCTION

The time an animal expends obtaining food and the geographical area that it must search to collect food are two important factors in determining the ecological relationship that exists between an animal and its environment. These temporal and spatial factors are the primary elements that determine an animal's foraging behavior (HAWKINS & HARTNOLL, 1983) and help delimit the individual's home range.

The rocky intertidal coast of Isla de Margarita, Venezuela, provides excellent locations for the investigation of activity differences among congeneric herbivorous limpets of the genus *Fissurella*. PRINCZ (1973) was among the first to document the abundance of *F. nimbosa* (Linnaeus, 1758) and *F. nodosa* (Born, 1778) along this coast. Together with *F. barbadensis* (Gmelin, 1791), which is also present (PRINCZ & GONZALEZ, 1981), these archaeogastropods exhibit significant movements or activity patterns during grazing periods.

When attempting to study animal feeding, both the temporal and spatial components of activity patterns must be considered (LITTLE, 1989). Temporally, animals may feed at different times during the day or night; in intertidal animals, these times may be related to such things as the rising or falling of tides. For example, *Tectura scutum* (Rathke, 1833) grazes upslope with the incoming tide and downslope with the outgoing wash (ROGERS, 1968). In addition to tidal considerations, mollusks can partition their environment with cyclic diel activity patterns, as was reported for the prosobranch *Nerita* in Panama (LEVINGS & GARRITY, 1983). *Lottia limulata* (Carpenter, 1864) shows sensitivity to both photoperiod and tidal cycles in its activity patterns, tending to move upward during nighttime incoming tides and downward during daylight changing tides (EATON, 1968).

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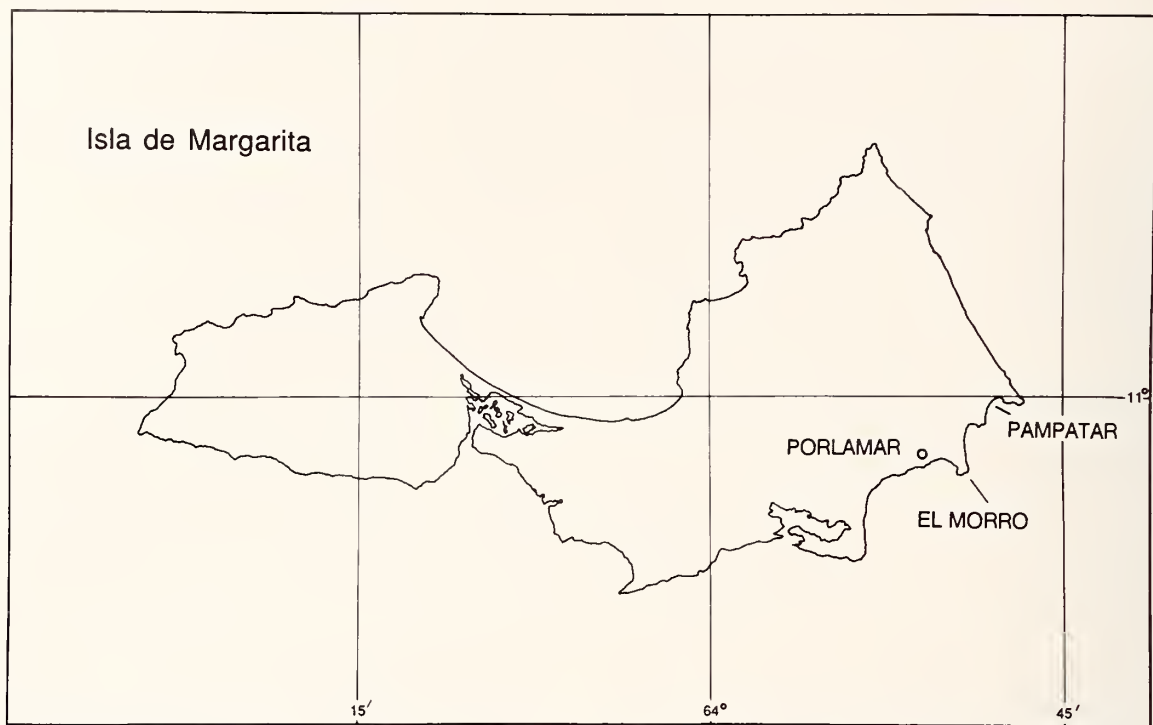
Figure 1

Map of Isla de Margarita, Venezuela, showing the locations of the two collection sites used during this study: Pampatar and El Morro.

The activity patterns of grazing animals also may have a spatial component: the animals may feed from particular locations or have regular search patterns instead of random patterns. The range of the feeding area, the placement of the animal's home scar within this range, and the magnitude of feeding excursions all provide information on how these limpets spatially utilize available resources. For example, the chitons *Acanthopleura brevispinosa* (Sowerby) and *A. gemmata* (Blainville) at low tide demonstrate temporal similarity in feeding, but spatial differences in the orientation and length of their feeding excursions (CHELAZZI *et al.*, 1983a). This permits the two co-occurring chitons to minimize zonal overlap, reducing the interspecific competition for food. Most of the members of the genus *Patella* partition their environment by occupying fixed positions on the shore, becoming established in one location and always returning to their own particular "home scar" (BRANCH, 1971). *Lottia pelta* (Rathke, 1833) exhibits spatial constraint in its feeding; it does not feed at random, but rather ingests specific alga types that are in abundance around the home site (CRAIG, 1968). An example of the complementarity of temporal and spatial aspects of activity patterns was seen in a study involving two co-occurring herbivorous neritid snails (LEVINGS & GARRITY, 1983). *Nerita funiculata* (Menke, 1851) forages from protected crevices for short times during ebbing and rising tides,

depleting algal crusts near their crevices. Unlike its congener, *N. scabricosta* (Lamarck, 1822) lives at upper tidal levels but moves down and grazes throughout the intertidal zone as the tide falls, returning as the tide rises again.

In temperate systems, dynamic physical conditions often mark the change of seasons. Air and water temperatures change, photoperiods shift with increasing darkness, and typically, tidal cycles change substantially in amplitude. In temperate climates, these physical parameters have a variability that may be used as cues to help regulate the timing and extent of feeding excursions (EATON, 1968; ROGERS, 1968). Conversely, tropical marine systems are constrained by relatively static physical conditions. For example, Isla de Margarita experiences little seasonal variability in the low-amplitude tidal flux, water and air temperatures, and day/night photoperiods. Under temperature conditions that show little seasonal variation, and in the absence of variable day-length photoperiodic cues, the tropical terrestrial prosobranch *Geophorus bothropoma* (Moellendorff, 1895) has a diurnal activity pattern (AUFFENBERG & AUFFENBERG, 1988). It is unknown whether seasonal, diurnal, or nocturnal responses exist in tropical Caribbean intertidal fissurellids as well.

Previous studies on the activity patterns of limpets frequently centered on the presence (FRANK, 1965; BREEN, 1971, 1972; RUWA & JACCARINI, 1986) or absence

(SUTHERLAND, 1970; RAO & GANAPATI, 1971; CREESE, 1980) of upshore and downshore seasonal migrations. Some earlier studies (MOORE, 1938; SOUTHWARD, 1964) attempted to relate grazing areas to animal size, but the sample sizes were small and the scope of the studies limited. No investigations have attempted to evaluate seasonal fluctuations existing in the grazing areas of limpets.

Although some information on *Fissurella barbadensis* exists concerning its feeding (WARD, 1966) and distribution in Barbados (LEWIS, 1960; WARD, 1968), the present study was conducted to provide more detailed documentation on the activity patterns of this grazer and its co-occurring congeners *F. nodosa* and *F. nimbosa*. Comparative ecological studies of the activity patterns of congeneric limpets may provide valuable insight into the manner by which these intertidal animals temporally and spatially partition their environment.

MATERIALS AND METHODS

The seasonal and diurnal activity patterns of *Fissurella nodosa, F. nimbosa,* and *F. barbadensis* were observed quarterly along the rocky intertidal zone of Isla de Margarita, Venezuela, between November 1987 and August 1988. The collection sites were El Morro (10°57.0′N, 63°49.0′W) and Pampatar (10°59.9′N, 63°47.4′W), both on the eastern coast of the island (Figure 1). These locations, which are subject to moderate wave activity, were chosen because large fissurellid populations occur there.

Vertical and horizontal quadrats were established on the rocks at the start of the study. The perimeter of these quadrats was delimited by nylon cords marked at 10-cm intervals. The corners of the quadrats were maintained by use of concrete nails driven into the rock. Limpet locations and movements were determined by measuring the horizontal and vertical coordinates of the animal. A "movement" was considered to be a change in geographical location of the limpet on the substratum over time (1 hr). Movement measurements were recorded to the nearest one-half centimeter. Fissurellids used in the studies were tagged by attaching wire markers (Thomas & Betts Corp., Raritan, NJ 08869) to the limpet shells *in situ* with a quick-drying gel acrylonitrite glue (Loctite Corp., Cleveland, OH 44128).

Observations for seasonal movements were made in the fall (November), winter (February), spring (May), and summer (August). The positions of the limpets within the quadrat were noted every hour for 24 continuous hours. Six animals of each species were observed. Distances between hourly movements were estimated by calculation of the straight-line distances between the two points. To avoid possible lunar influences on activity patterns, seasonal collections were always made within two days of a full moon.

The 24-hr coordinates of each limpet were printed graphically and grazing areas were determined by an Olympus (CUE 2) computerized image-analysis program. Because the computer scans only closed polygons, in cases where the animals did not return to their home scar, grazing areas were artificially closed by graphical connection of the outlier with its nearest neighbor.

Limpet shell measurements were obtained by using Vernier calipers to obtain length, height, and width. The volume was determined using CUBIT's (1984) method of inverting the shells and filling them with a 50:50 ethanol : water mixture, which has less of a meniscus than pure water.

After a 24-hr observational period, the animals were detached from the rocks and preserved in 70% ethanol. During October 1987, ash-free dry weight determinations of all animals were made using a Type 1500 Thermolyne Electric Furnace (Thermolyne Sybron Corp., Dubuque, IA 52001). To avoid treatment effects due to limited furnace space, the limpets were randomized into lots of 10 each. All were processed similarly: the animals were dried for 24 hr in a drying oven at 100°C, cooled in a desiccator, weighed, dried in pre-ashed containers for 12 hr at 500°C, and finally cooled in a desiccator and weighed again. The final mass was subtracted from the dry mass of the bodies. Weights were taken to four decimal places utilizing a Mettler AC 100 balance.

Commencing on 27 February 1987, and lasting a complete lunar cycle, the limpet movements were recorded hourly for 24 continuous hours on alternate days. Fifteen animals initially were selected for study, but during the course of the observations, three were lost to natural causes; therefore, 12 individuals were utilized in the calculations. Lunar cycles, limpet movements, times of movement, and tidal patterns were observed throughout this part of the study.

Tidal data for the observational periods were obtained from the MINISTERIO DEL AMBIENTE Y DE LOS RECURSOS NATURALES RENOVABLES (1986, 1987). Isla de Margarita experiences diurnal tidal cycles that have a daily amplitude of slightly less than one-half meter. During the study period, the greatest tidal height was recorded in December 1986 (+0.43 m) and the lowest in June 1987 (−0.13 m). Statistical analyses were performed on Systat software (Systat Inc., Evanston, IL 60202).

RESULTS

Seasonal and Diurnal Studies

The results of the present investigation indicate that all three species of *Fissurella* return to a home scar after foraging. *Fissurella barbadensis* exhibited homing in 90% of the diurnal observations ($n = 180$). Subjective assessments (*cf.* UNDERWOOD, 1979) estimated that 80–90% of *F. nimbosa* and 30–40% of *F. nodosa* exhibit homing behavior (personal observation). Homing in limpets often results in the establishment of a distinctive rock scar into which the contours of the limpet shell fit with great precision. In *Fissurella,* the tightly fitting home scar is usually located in the center of the foraging area (Figure 2) around which
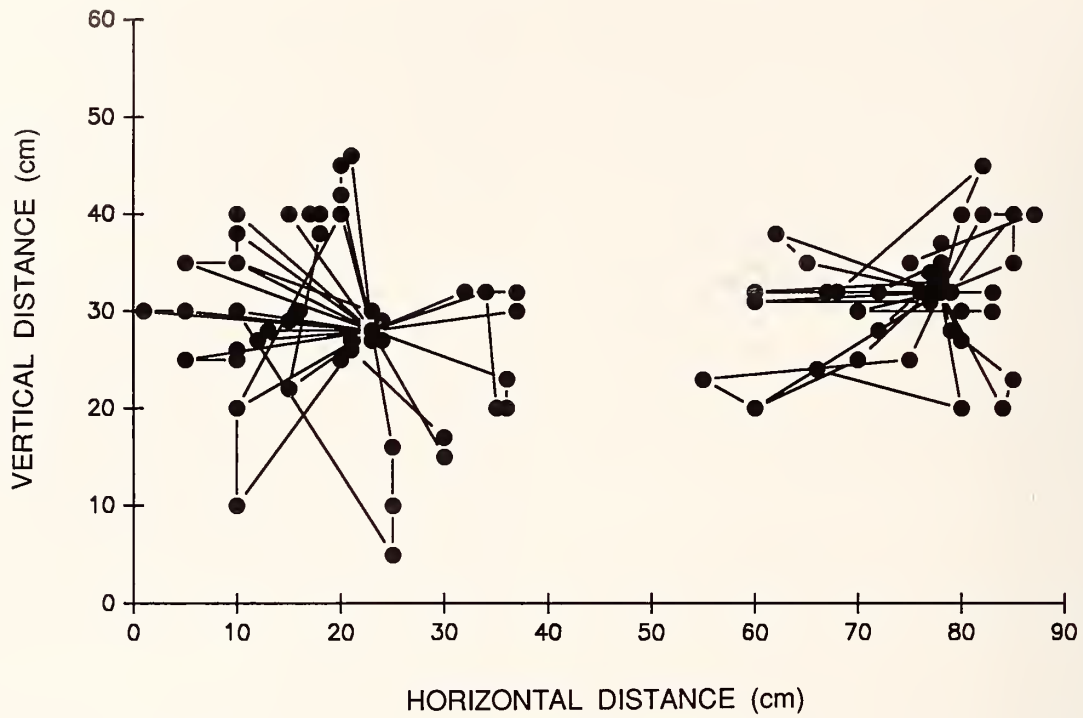
Figure 2

Activity patterns of two individuals of *Fissurella barbadensis* at El Morro, Isla de Margarita, Venezuela, during 13 days and nights in March 1987. Dots represent the actual coordinates of the limpets on a vertical rock surface during hourly observations. Axes indicate vertical and horizontal coordinates during observation intervals.
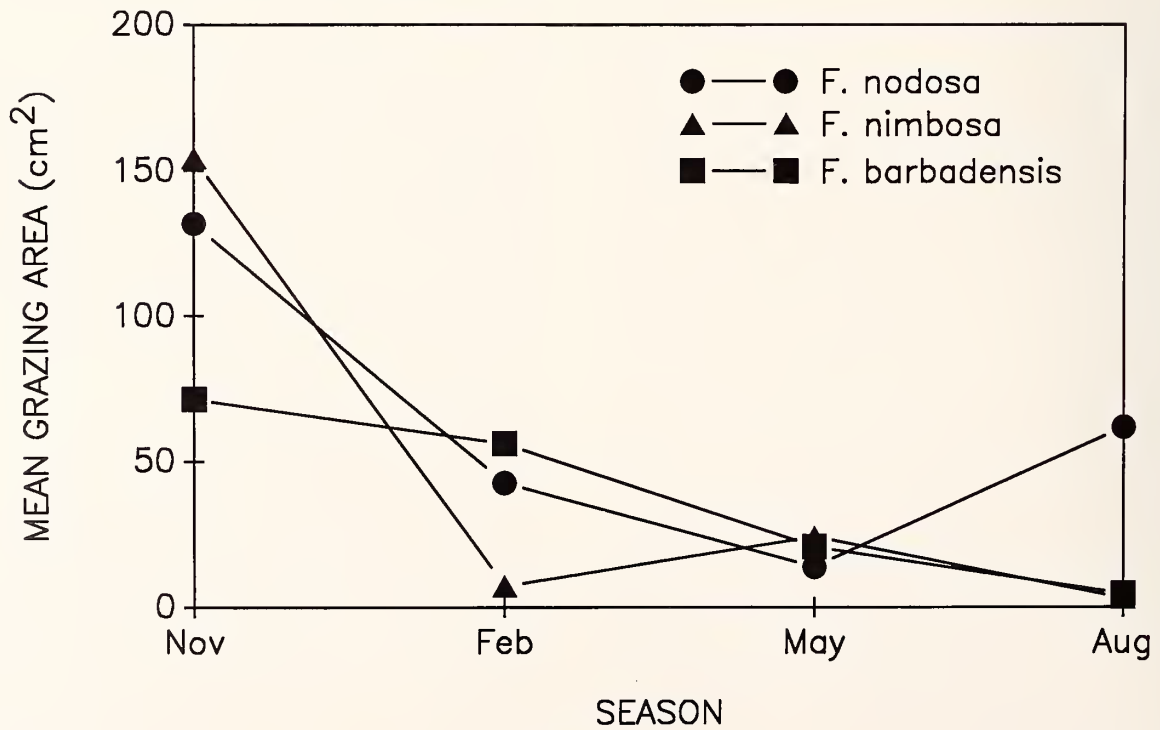

Figure 3

Seasonal differences of three *Fissurella* spp. in their mean grazing areas (GA).
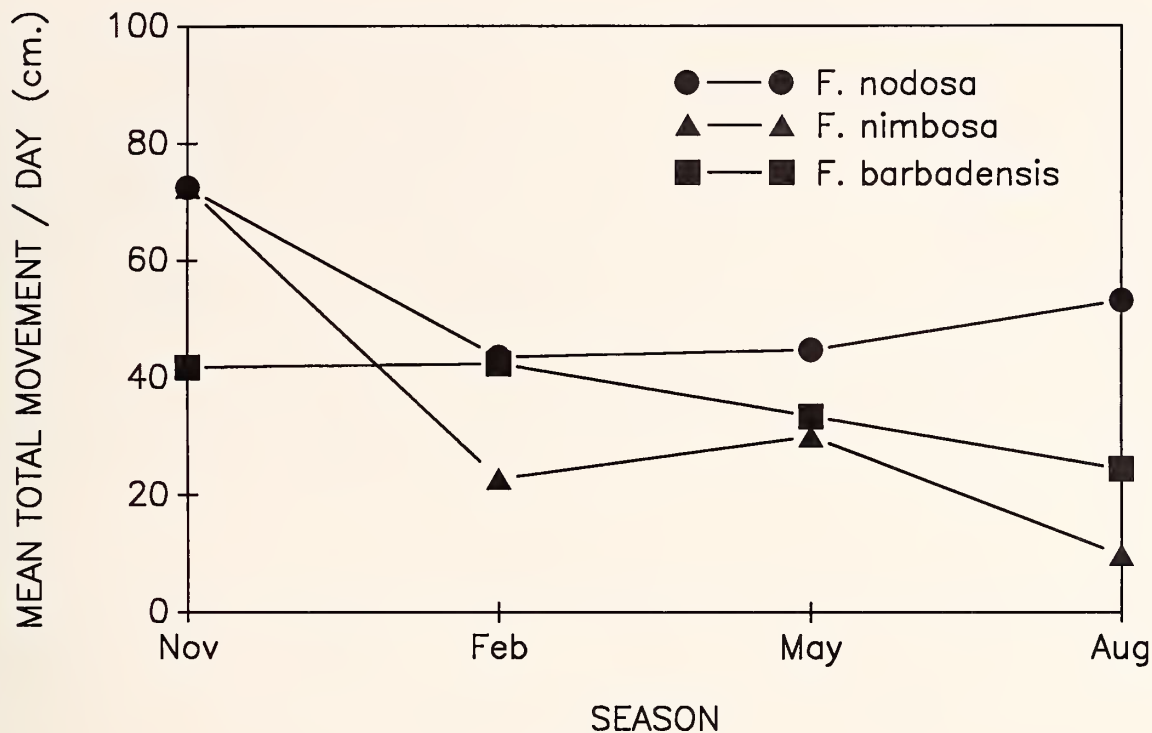
Figure 4

Seasonal differences of three *Fissurella* spp. in the mean length of total movements (TM) on vertical surfaces during 24-hr observation periods.

feeding takes place in a 360° arc. When they return to the home scar, fissurellids position themselves exactly as oriented prior to departure. There were no tendencies among the three species of fissurellids to establish a home scar orientation (up, down, east, west, etc.) ($\chi^2 = 1.57$, n = 114).

Analysis of the limpet grazing areas (GA) indicates that significant seasonal effects exist (2-way ANOVA, d.f. = 60, $P = 0.001$) (Figure 3). Although all three species of *Fissurella* had their largest GA values during the fall season and their lowest during the spring, significant differences were found neither among species ($P = 0.398$) nor in the interactions between species and seasons ($P = 0.172$). Accordingly, *F. nimbosa, F. nodosa,* and *F. barbadensis* all can be assumed to have grazing areas of approximately the same magnitude.

Analyses of the total movement (TM) distances of animals during 24-hr intervals indicate that, regardless of season, *Fissurella nodosa* consistently has greater TM than *F. barbadensis* or *F. nimbosa* (Figure 4). Season (2-way ANOVA, d.f. = 60, $P = 0.001$), species ($P = 0.002$), and interaction ($P = 0.029$) effects are significant for TM: the distance moved depends on both the species and season. Linear contrasts fail to discriminate between *F. nimbosa* and *F. barbadensis,* indicating that *F. nodosa* has different TM values than the other species. Whereas mean values

for TM of *F. nimbosa* and *F. barbadensis* are similar, a high variance is found for *F. nimbosa* because occasionally no movement is found during a given 24-hr period; at other times, there may be relatively long feeding excursions. This phenomenon for *F. nimbosa* has been reported elsewhere (FRANZ, in press a).

An analysis of the number of movements (NM) an animal makes per diel cycle indicates significant species (2-way ANOVA, d.f. = 60, $P = 0.001$), season ($P = 0.022$), and interaction ($P = 0.016$) effects (Figure 5). The overall average of movements for *Fissurella nodosa* (6.6 movements/24 hr) was greater than the other species; except in the fall, *F. nodosa* seasonally averaged a greater number of movements per day than the other limpets. Its excursions varied from a greater NM during the fall and spring to a lower NM during winter and summer. Even with a high fall value for movement by *F. nimbosa*, there was no difference in the mean NM between this limpet and *F. barbadensis*; both *F. nimbosa* and *F. barbadensis* averaged approximately 4.5 movements per 24-hr period. Because measurements were taken at hourly intervals and realizing that these animals feed primarily while moving, these measurements of movement may additionally reflect the number of hours the animals graze on a daily basis. However, these animals may occasionally feed while not moving and this measurement is most likely an underestimate of feed-
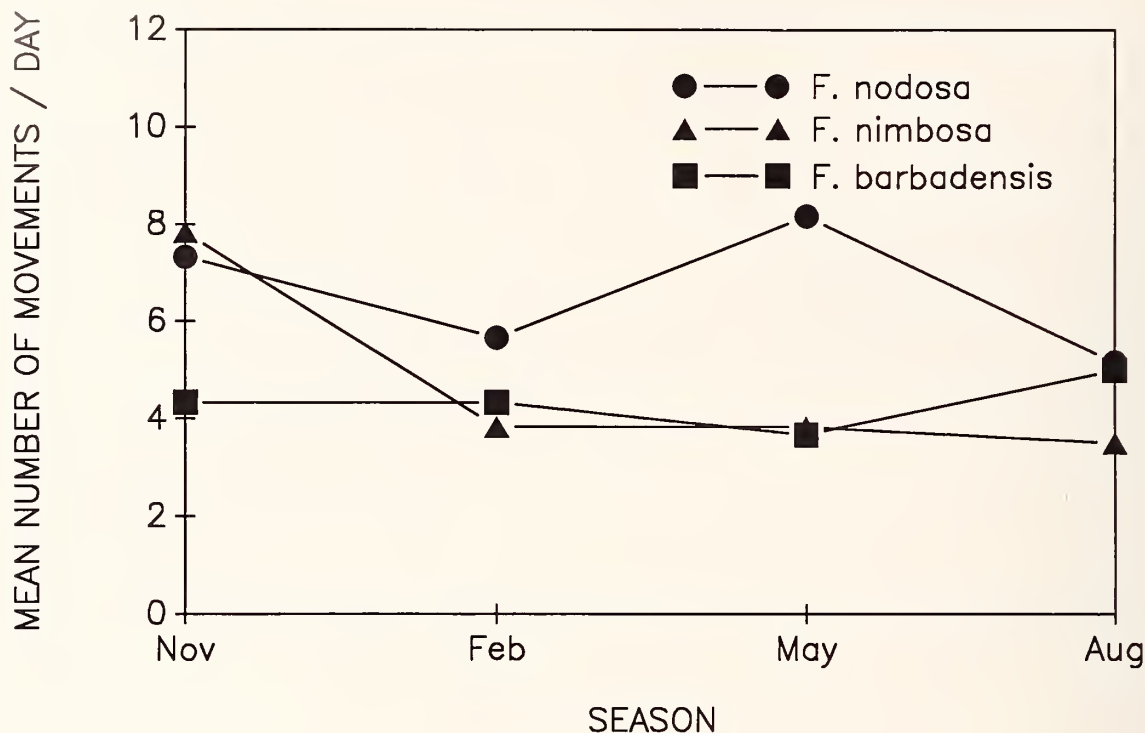
Figure 5

Seasonal differences of three *Fissurella* spp. in the mean number of movements (NM) on vertical surfaces during 24-hr observation periods.

ing time. Rarely have I observed them moving without foraging.

Investigations of the average movement lengths (ML) of a given limpet during a feeding excursion, determined by dividing the sum of the lengths by the number of movements, yielded no significant differences between the seasons (2-way ANOVA, d.f. = 60, $P = 0.082$). Differences among the fissurellid species ($P = 0.003$) and interactions ($P = 0.001$) indicate that ML depends on both species and season (Figure 6). The relatively consistent seasonal trends for average movement lengths among all three *Fissurella* showed a marked decline in their summer values. The mean values for *F. nodosa, F. nimbosa,* and *F. barbadensis* were 8.84 cm, 5.93 cm, and 8.58 cm, respectively; linear contrasts failed to separate the average movement length of *F. nodosa* from those of *F. barbadensis*. The interaction effect is most probably due to the differences in spring and summer movements; for all three species, tests for the difference between means during these months were significant at the $P = 0.05$ level.

Individuals of *Fissurella* may travel great distances in their feeding excursions. Maximal hourly movements of 57 cm were witnessed for *F. nodosa,* while both *F. barbadensis* and *F. nimbosa* moved as far as 26 cm in an hour.

An analysis of the physical characteristics of each species was conducted. This analysis included measurements of length, width, height, volume of the shell, dry weight of the animal, and ash-free dry weight of the animal. In the present study of intertidal archaeogastropods, these variables showed relatively high Pearson correlation values (Table 1). The dry weights and ash-free dry weights were strongly correlated ($r = 0.994$). These physical dimensions were uncorrelated with grazing area, however.

Among the three species of *Fissurella,* there was temporal partitioning of grazing excursions. A total of over 240 daily observations were made of individual fissurellids during which time a total of 1136 movements were recorded. After separation of data by species, the data were subdivided into two groups depending upon whether the grazing activity occurred during the day (0700 to 1800 hr) or night (1900 to 0600 hr). Thirty-nine percent of the feeding excursions for *F. nimbosa* occurred during daylight hours while *F. nodosa* did 76% of its feeding during that time. For both species, there was no difference in the average distance a limpet moved during its feeding excursions when diurnal and nocturnal values were compared. Additionally, both species fed most intensely during periods of rising tides (Table 2). *Fissurella barbadensis* was primarily a nocturnal grazer: 98.7% of the movements of this animal occurred during the night interval between 1900 and 0600 hr.

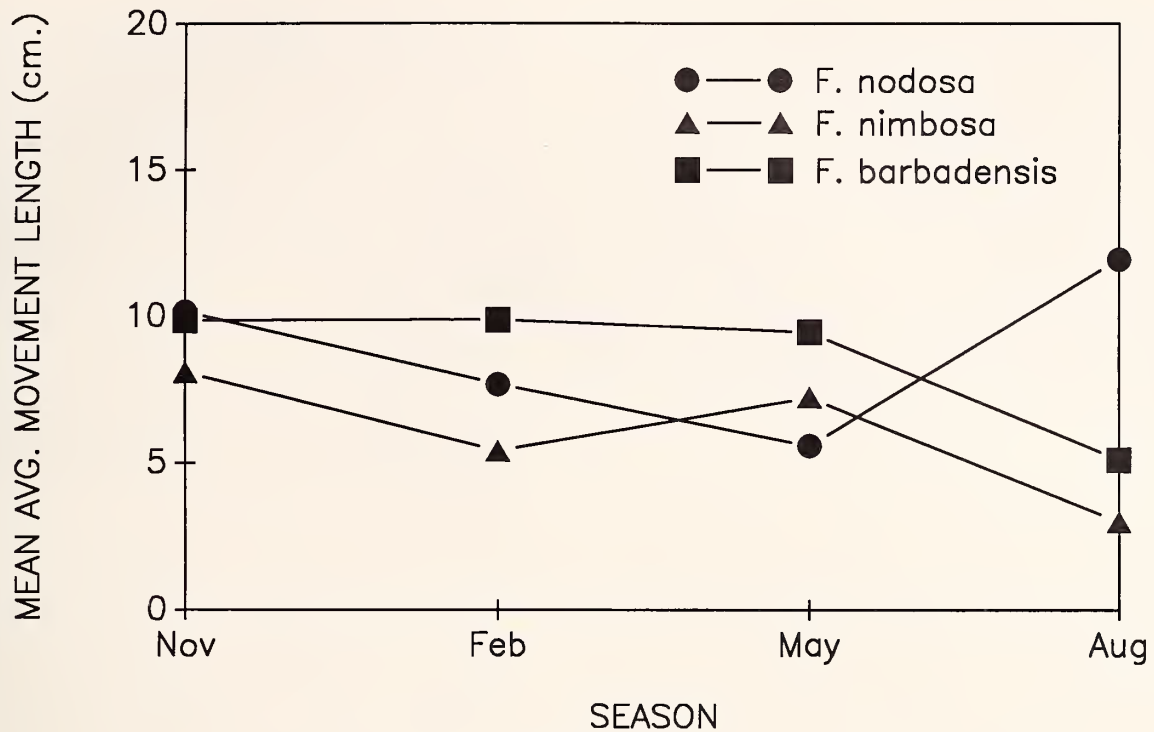*Fissurella* exhibited no apparent pattern to the direction

Figure 6

Seasonal differences of three *Fissurella* spp. in the mean movement length (ML) on vertical surfaces during 24-hr observation periods.

in which foraging occurred after leaving the home scar. The limpets were as likely to move upward as downward, or to the right as to the left; on subsequent nights, feeding excursions would be in different directions. Although CONNOR (1986) reported that the homing limpets *Lottia gigantea* and *Collisella scabra* capitalize on their food-en- hancing mucus by retracing their trails, *F. barbadensis* exhibited little iteration over a given trail during a month of observed activity. There was no evidence of increased macrophytic growth on fissurellid trails.

Nocturnal Studies

Fissurella barbadensis was used to study the effects of lunar cycles on limpet feeding behaviors. This species was chosen because it is almost exclusively nocturnal and has

Table 1

Pearson correlation matrix of body dimension data and grazing areas for *Fissurella* spp. ($n = 72$ individuals) collected from Isla de Margarita, Venezuela during 1986 and 1987. Abbreviations are for shell length (LGTH), shell width (WDTH), shell height (HGTH), shell volume (VOL), animal dry weight (DRYWT), ash-free dry weight (ASHWT), and grazing area (AREA).

	LGTH	WDTH	HGTH	VOL	DRY WT	ASH WT	AREA
LGTH	1.000						
WDTH	0.969	1.000					
HGTH	0.858	0.862	1.000				
VOL	0.947	0.936	0.879	1.000			
DRYWT	0.865	0.863	0.884	0.924	1.000		
ASHWT	0.873	0.868	0.900	0.931	0.994	1.000	
AREA	0.151	0.144	0.163	0.184	0.063	0.080	1.000

Table 2

Percentage of feeding excursions of *Fissurella* on Isla de Margarita, Venezuela, during different aspects of the tidal cycle. Data were collected between November 1986 and August 1987; the movements were recorded hourly for complete tidal cycles. The total number of movements, from which these percentages are derived, are listed in parentheses.

Species		Tidal condition			
		High	Falling	Low	Rising
F. nodosa	($n = 210$)	0.148	0.224	0.133	0.495
F. nimbosa	($n = 126$)	0.119	0.270	0.175	0.436
F. barbadensis	($n = 146$)	0.528	0.207	0.007	0.257

a clearly discernible home scar. Although the shell of these limpets may be covered with algal growth and blend into the environment well, an animal's absence from its home scar is easily recognizable. During the 13-hr period from 1900 to 0700 hr, *F. barbadensis* was active for an average of 4.5 hr. Generally speaking, these animals grazed most actively between midnight and 0500 hr; of the movements observed during the one-month sample period, 70.2% of them occurred during these hours. Among individuals of *F. barbadensis,* a trend was apparent towards more intense grazing activity at later hours during a new moon and earlier hours during an old moon. During a full moon, the limpets had intermediate feeding times between 1900 and 0600 hr.

DISCUSSION

The extent to which animals establish grazing areas around their home scar is dependent upon a number of interrelated variables: locomotory rate, turning angles, frequency of turns, stops, lengths of straight components, total path length, randomness or straightness, and end-point location (SINIFF & JESSEN, 1969). The interrelation of these spatial variables is particularly relevant in the activity patterns of intertidal fissurellids. *Fissurella nimbosa* and *F. barbadensis* have approximately the same number of movements, length of movements, total distance travelled, and grazing area. Contrarily, *F. nodosa* exhibits greater movement lengths and number of moves, yet its grazing area is the same as the other congeners studied. Amid these diverse combinations of geometric parameters, it is enigmatic why the seasonal grazing areas of *Fissurella* spp. are similar and why interactional effects are absent. Among other activity patterns, 2-way ANOVAs for TM, NM, and ML indicate the presence of interactions. Obviously, a complex spatial relationship exists among movement variables in fissurellid activity patterns. I suspect that differential foraging techniques (FRANZ, in press a) and unique food preferences (FRANZ, in press b) may influence fissurellid activity patterns.

Temporal conditions also influence activity patterns. Similar to the limpet *Collisella scabra* (Gould, 1846), *Fissurella nodosa* feeds during the day. *Fissurella nimbosa* feeds both during the day and at night as do *Cellana toreuma* (Reeve, 1855) (HIRANO, 1979), *Lottia limulata* (WELLS, 1980), *Tectura scutum* (Rathke, 1833) (ROGERS, 1968), *Siphonaria normalis* (Cook, 1969), *S. alternata* (Say, 1822) (COOK, 1971), and *S. pectinata* (Linnaeus, 1758) (THOMAS, 1973). An earlier investigation conducted on Barbados reported that *F. barbadensis* fed periodically throughout the night and day (WARD, 1966); however, the present study indicates that *F. barbadensis* is almost exclusively a nocturnal feeder. Such activity may minimize visual identification by predators (*cf.* LEVINGS *et al.,* 1986), although this hypothesis was not tested.

A number of mollusks (BRANCH, 1981; HAWKINS & HARTNOLL, 1983; LITTLE, 1989) and crustaceans (JANDER,

1975; VERNBERG & VERNBERG, 1983) have tide-influenced grazing patterns. *Fissurella nodosa* and *F. nimbosa* show the greatest feeding activity when awash during rising or falling tides; *F. barbadensis* feeds principally while submerged. Such behavior may be due to differential desiccation tolerance among the congeners.

Homing is a well-established phenomenon in many genera of limpets including *Siphonaria* (COOK, 1969, 1971; COOK & COOK, 1975), *Patella* (BRANCH, 1971), *Collisella* (JESSEE, 1968), *Lottia* (STIMSON, 1970), *Cellana* (UNDERWOOD, 1977), and *Fissurella* (WARD, 1966). Homing behavior has been observed in chitons such as *Liolophura* (NISHIHAMA *et al.,* 1986), *Sypharochiton* (KNOX, 1963), *Acanthopleura* (CHELAZZI *et al.,* 1983b), and *Acanthozostera* (THORNE, 1968). Among the congeneric limpets studied here, homing was more strongly exhibited by some species than others: *F. barbadensis* > *F. nimbosa* > *F. nodosa.*

The selective advantage of homing is uncertain; however, this behavior may serve to avoid predation (PHILLIPS & CASTORI, 1982; GARRITY & LEVINGS, 1983; KUNZ & CONNOR, 1986) and optimize algal resources (HAWKINS & HARTNOLL, 1983). Hence, the location of a fissurellid home in the center of the foraging area may provide protection and an efficient initiation point for subsequent excursions. Other researchers have suggested that homing may minimize desiccation (VERMEIJ, 1973; BRANCH, 1981; VERDERBER *et al.,* 1983; GARRITY, 1984), but this would make sense only for species that live high on the intertidal zone. Because *Fissurella* exhibits an inverse relationship between homing and intertidal height of the home scar, the avoidance of desiccation is unlikely to be the primary explanation for homing in these limpets.

UNDERWOOD (1979) suggested that homing behavior maintains a pattern of density dependent distribution which leads to even dispersal of the population. Subsequently, maximal utilization of food resources can be achieved by partitioning the available food supplies. Indeed, density dependent assemblages of *Fissurella virescens* Sowerby have been reported along the Pacific coast of Costa Rica (ORTEGA, 1985). Although the present study was not designed to examine competitive relationships among species, data collected from the lunar study indicate that *F. barbadensis* forms grazing territories. Where two individuals are neighboring, there appears to be spatial partitioning of the available food resources by establishment of discrete home ranges (Figure 7). Although some overlap of foraging areas occurred, the grazing area boundaries of an individual limpet were generally well respected. Other limpets such as *Lottia gigantea* Sowerby, 1834 (STIMSON, 1970, 1973) and *Patella longicosta* (Lamarck) (BRANCH, 1975b) defend their territories rigorously, but this was never observed for *Fissurella.*

Unlike other species such as *Lottia digitalis* (Rathke, 1833) (MILLER, 1968) and *L. gigantea* (ABBOTT, 1956) which orient with their head facing downward on vertical or nearly vertical rocks, there were no tendencies among
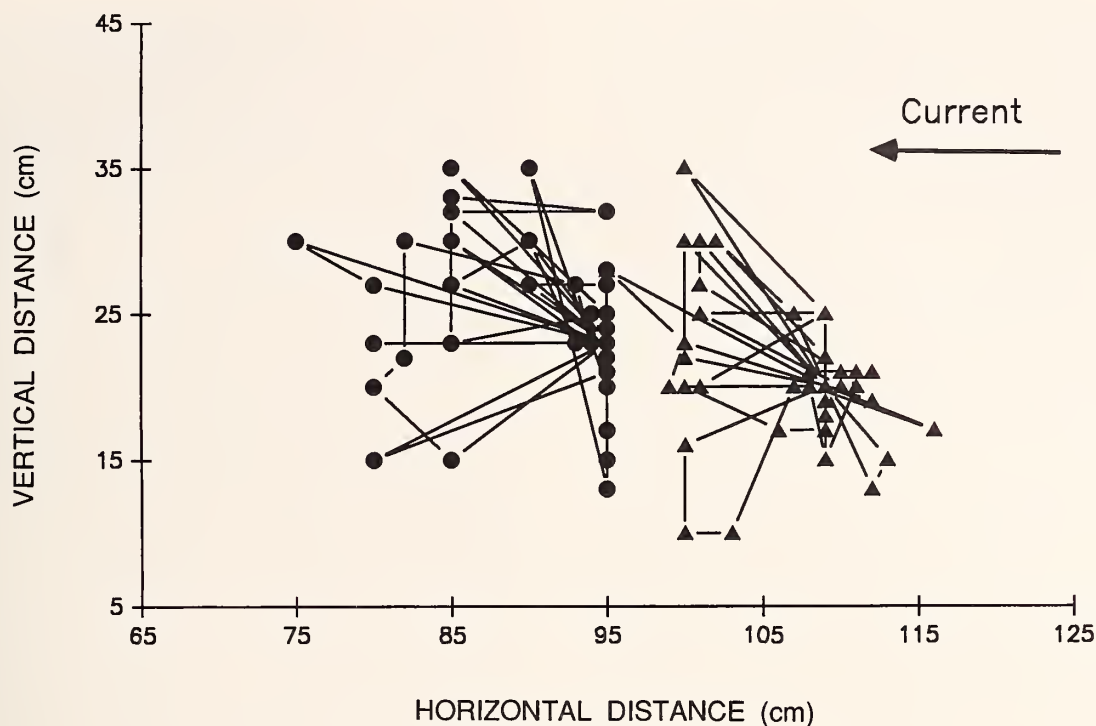
Figure 7

Movement patterns of two individuals of *Fissurella barbadensis* at El Morro, Isla de Margarita, Venezuela, during 13 days and nights in March 1987. Dots and triangles represent the actual location of the two limpets on a vertical rock surface during hourly observations. A persistent and very strong current probably caused the noticeably asymmetric grazing pattern.

Fissurella spp. to orient in a particular direction when on their home scar. COLLINS (1976) reported that in *Collisella scabra* the inclination angle of the substratum may influence the potential for desiccation and this topographical feature may influence distributional patterns. In the present study, *F. nodosa* and *F. nimbosa* were almost always located on a vertical wall, frequently homing close to algal tufts that provided shading during low tide periods and protection from impacting waves. *Fissurella barbadensis* was found typically on flat, subtidal rock platforms.

Studies on prosobranch limpets (BRANCH, 1975a; BRETOS, 1982) have indicated that high correlations may exist among such characters as height, length, width, volume, dry weight, and ash-free dry weight. Indeed, among these characters, strong relationships were found for *Fissurella nodosa, F. nimbosa,* and *F. barbadensis*. Although significant statistical relationships have been found between body size and grazing areas in terrestrial mammals (SWIHART *et al.,* 1988) and between shell length and grazing distances for Japanese limpets (HIRANO, 1979), such relationships were not found among *Fissurella*. Failure to find a significant linear association between animal size and grazing distances has been reported by COOK & COOK (1981) for *Siphonaria* limpet populations.

Although the congeneric variations noted above would

tend to suggest micro-partitioning of the environment on both spatial and temporal scales, additional experiments involving manipulations of limpet densities together with exclusion and replacement studies are needed to fully evaluate the impact that variable activity patterns have on fissurellid co-occurrence along the Venezuelan intertidal zone.

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